PAN-PACIFIC ENTOMOLOGIST
65(4), 1989, pp. 429–435

Temporal and Spatial Distribution of the Camel Cricket, *Farallonophilus cavernicola* Rentz (Orthoptera: Gryllacrididae), on Southeast Farallon Island, California

JOHN STEINER

Department of Biological Sciences, California State University, Hayward, Hayward, California 94542.

The habits and habitat of *Farallonophilus cavernicola* (Orthoptera: Gryllacrididae) are of interest because of this camel cricket's restriction to the Farallon Islands and its possibly primitive taxonomic status relative to the abundant, widespread *Pristoceuthophilus pacificus* on the adjacent mainland of central California. Although Rentz (1972) described the cricket from the "Rabbit Cave" on Southeast Farallon Island, he was limited by time and did not thoroughly investigate the complete distribution of the insect. During two brief visits, he found the cricket to occur only inside the cave, except for one specimen under a rock, "100 yards from the cave entrance." Though he searched the island for additional locations, he was unable to find the cricket anywhere else.

In September and October 1987 and April 1988, I investigated the biology of *Farallonophilus cavernicola* by conducting two week-long studies. During fall 1987, I searched through all accessible caves and holes and surveyed the cricket's distribution. During spring 1988, I studied cricket behavior in two of the island caves.

The Farallon Islands form an archipelago of weathered granitic rocks and small, terraced islands at the edge of the continental shelf west of the Golden Gate (Fig. 1). The largest of these is Southeast Farallon Island (Fig. 2) at position 32°47′W, 123°00′N, having a surface area of 44 ha.

This island is predominantly rocky, nearly treeless, and covered during much of the year with farallon weed, *Baeria maritima,* which grows in profusion during the spring and summer. The island consists of granitic cliffs, spires and talus slopes, as well as boulder fields on the marine terraces. It has dozens of ancient surge caves formed by waves during periods of higher sea level. Now at an elevation of 15 m or higher (Fig. 2), the caves are dark, cool and damp.

Point Reyes Peninsula, 32 km north in Marin County, and Montara Mountain, 44 km east in San Mateo County, have Salinian Block granitic substrate similar to Southeast Farallon Island (Compton, 1966). During Pleistocene sea level lowering, the island must have been connected to the mainland (Fig. 1, showing bathymetric contours). Southeast Farallon Island was probably severed from Point Reyes and Montara Mountain about 8000 yr BP by rising sea level (Milliman and Emery, 1968). Wingless insects on Southeast Farallon were then probably isolated from those on the mainland.

Partial descriptions of the insect fauna began with Blankenship and Keeler (1892) who studied larger animals, but included a list of 11 insect species. Later studies by Marshall and Nelson (1967), Giuliani (1982) and Schwan (1984) doc-

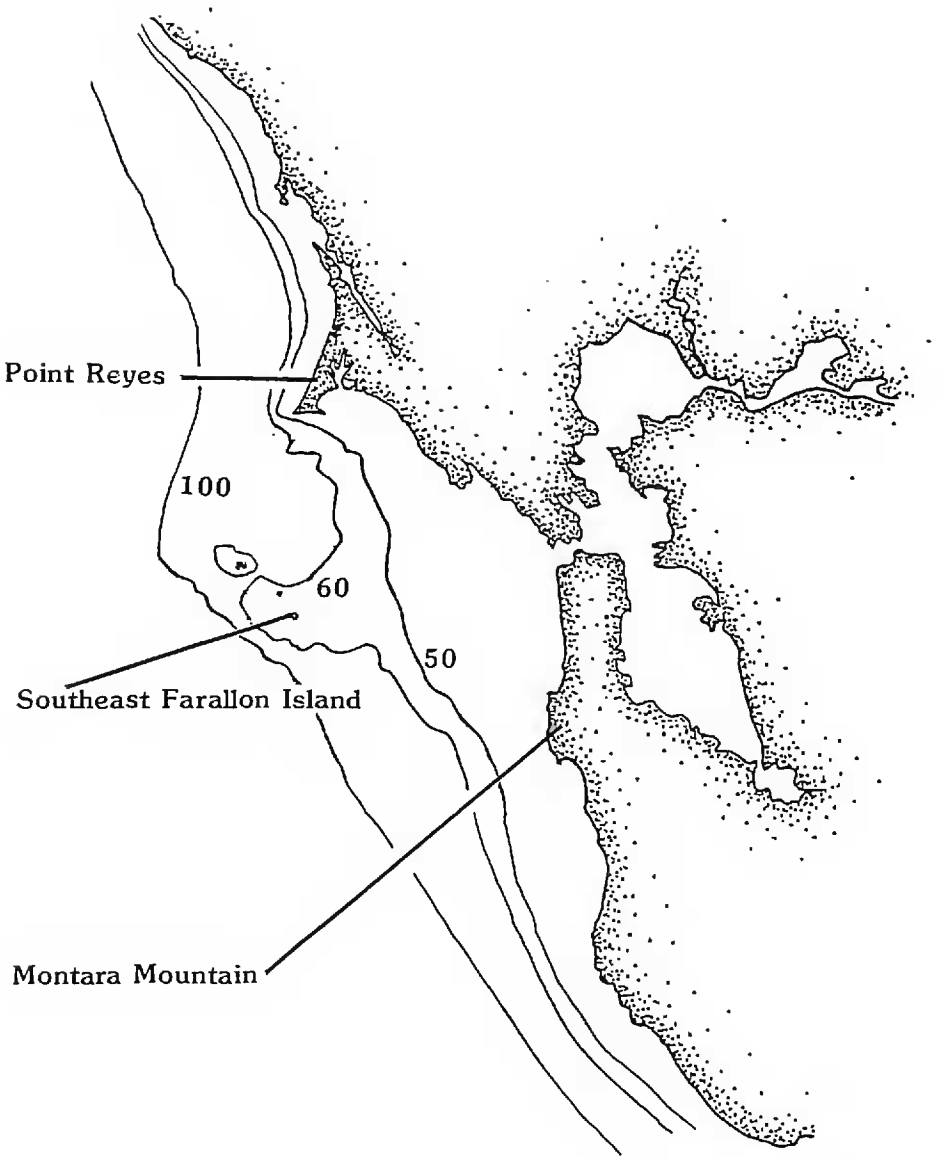

Figure 1. Location of Southeast Farallon Island. Bathymetric contours in meters.

ument additional insect species on the island. A comprehensive insect list (Steiner, in prep.) is not yet ready. Rentz described *Farallonophilus cavernicola* in 1972 and discussed its basic distribution and biology. This paper analyzes a diel activity pattern unique among camel crickets, and reports a broader spatial distribution.

Methods

I investigated 10 different surge caves (Fig. 2) on Southeast Farallon Island by either crawling into them or by visually inspecting the inner reaches of the smaller holes with my flashlight. I made the rounds of each of the caves several times during daylight and dark periods. I repeatedly stayed inside certain caves for up to an hour to make notes of insect behavior and to observe the interactions of crickets and the Cassin's auklets (burrowing alcid seabirds) which also occupied the caves. I tried to minimize disturbance to either the camel crickets or the auklets during my movements within the caves by crawling slowly and keeping my flashlight off until I was positioned. My hand covered the flashlight lens when I turned the light on, to prevent a sudden flash of light. I mapped the locations of every cricket on the walls and ceiling of each cave (crickets did not occur on cave floors) to determine the extent of movement by individuals between successive visits.

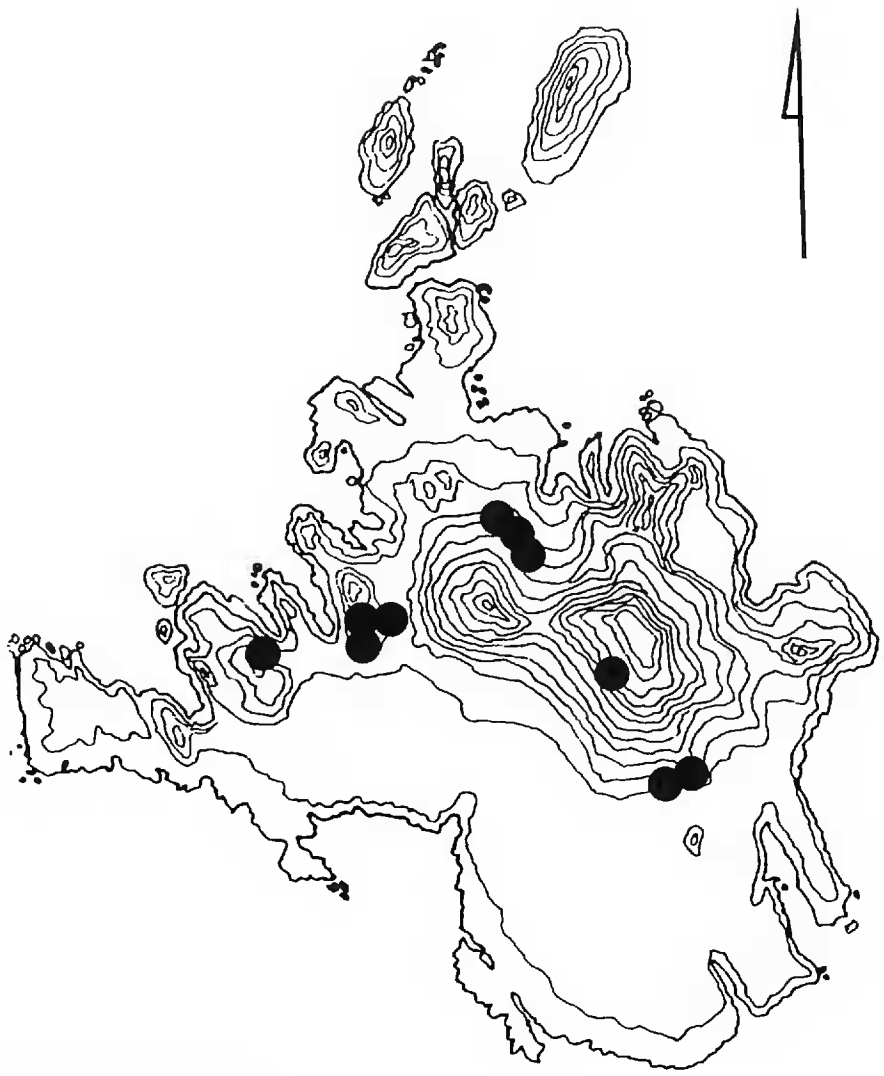

Figure 2. Southeast Farallon Island. Surge caves indicated by dark circles. Contour lines depict 6-m intervals.

Ledges, cliff faces and seabird burrow entrances were baited with uncooked, dry oat flakes to assess the presence of crickets outside of the caves. As part of another project, I ran five transects across the marine terraces or up talus slopes and overturned boulders at each of 20 random points along each transect, looking for insects underneath. Camel crickets were preserved in 70% ethanol and voucher specimens deposited at California Academy of Sciences and in the University of Michigan Museum of Zoology. Insects other than camel crickets and various larvae were pinned and dried.

Activity

Farallonophilus crickets exhibited a definite, consistent circadian rhythm in their activity periods. During the day, from just before sunrise throughout the daylight hours until about an hour after sunset, crickets were quiescent. They perched on the walls and ceilings of the caves as described by Rentz, mostly in groups of up to 12 individuals (Rentz counted up to 15 insects per group). Though there was much contact via antennae, not all crickets in a group touched other crickets. During this quiescent period, the antennae were still; repeated checks throughout the day failed to show any change in position in most crickets. One

or two insects in a group may have changed position during the course of the day, but never traveled more than 2–3 cm from their original positions before resuming their inactive stance.

Observations during successive daylight periods revealed groups of quiescent crickets occupying the same areas within the caves. The numbers of crickets within the group in a given area changed from day to day, but each area occupied was the same. All crickets were absent from the areas during their active periods. Such favored sites were concave depressions and hollows on the ceilings and upper walls of the caves.

Individual movement began shortly after sunset. Crickets appeared still quiescent, their antennae motionless, but they occupied different nearby sites during successive inspections. Most activity occurred during early morning hours. From about 0400 until sunrise at about 0600, the crickets scurried about on the rock surfaces and waved their antennae. Some traveled to the outsides of the cave entrances. Up to eight insects were found on the cliff walls around one of the caves within 1 m of the cave opening. I did not observe any of the camel crickets feeding. The insects became quiescent again at dawn.

I noticed many more changes in location and position at night than during the day. If cricket movement during the quiescent period was due to disturbance caused by my entering the caves, increased nighttime movement may have been due to an increased level of alertness. Though more individuals had repositioned themselves between successive nighttime checks, they were motionless during inspection. This sequence of events was the same during both of my visits, during fall and spring. Though I did not undertake a precise study of activity during my 1987 visit, I did make general observations, and noted that the insects were most active from 0400 until dawn, during which time some left their caves. This behavior is directly counter to what Rentz (1972) found. Studying *Farallonophilus cavernicola* in vivaria, he demonstrated greater activity, and even observed mating, in the late afternoon.

This short activity period described here is also contrary to that discovered by other researchers, for other camel crickets (Campbell, 1976; Cohn, pers. comm.), *all* of which began activity immediately after dark (Cohn, pers. comm.).

The effect of my crawling in and out of the caves on the presence and activity levels of the camel crickets is hard to estimate. If that effect is the same regardless of time of day, differences in degree of activity between different times reflect diel behavior of the crickets. I took care to minimize disturbance to the insects, but I did notice minor movement. On one occasion I saw a cricket slowly moving away from the spot where I had found it earlier, as I increased the illumination in the cave. All other insects remained in their prior locations, their antennae in the same positions. The moving cricket stopped 2 cm away and became motionless again. Checks later in the day showed no further movement.

No crickets took the oatmeal bait which attracts all other North American camel crickets. Cohn (pers. comm.) suggests that the fog-dampened oat flakes may fail to attract the crickets. The moist flakes did attract many *Eleodes* beetles.

Habitats

Farallonophilus cavernicola is found in several habitats on Southeast Farallon Island. It occupied all 10 different surge caves, occasionally visited cliff faces, and it occurred in auklet burrows, wooden observation blinds and other habitats.

These habitats were diverse in nature and widespread in distribution, but all are damp and cool. No other insects were observed near the crickets.

Crickets were most abundant on the walls and ceilings of the caves. Some left the caves after 0400, and ran about outside on the cliff face within 1 m of the cave entrance. Cracks in the cliffs and talus provided cover. Whether these cracks communicate directly with cracks inside the caves is unknown; crickets probably come and go via the mouth of the cave itself.

In October 1987, while overturning boulders along a transect on the north side of the island, I accidentally uncovered two Cassin's auklet burrows. Each contained a single cricket. No other burrows were examined. Surprisingly, Udvardy found no crickets in the many auklet burrows that he excavated (pers. comm. *in* Rentz, 1972). I turned over 20 boulders at random points along each of five different transects, and found no camel crickets under boulders that did not cover burrows, but Rentz found a single cricket under such a boulder. I did see up to 17 *Coniontis* beetles under each boulder, as well as *Eleodes* and other insects. Perhaps the camel crickets have been displaced from most boulders by the abundance of beetles. *Farallonophilus cavernicola* was not discovered by the above series of investigators, who no doubt looked under boulders in search of insects, until Rentz found it in surge caves.

These camel crickets are known to occur in other island habitats. In October 1987, I found a cricket in a wooden observation blind, next to the ceiling behind a window shutter where the wood is cold, dark, moist and covered with moss. Resident biologists on Southeast Farallon Island have occasionally seen them during wet weather crawling through the Farallon weed that covers the island. Camel crickets have also been seen in a pile of wet shingles under the dripping eaves of a residence building (R. P. Henderson, pers. comm.). The crickets are probably able to expand their range during the wet season each year, and exploit habitats unavailable to them during the dry season, when desiccation would result from wandering too far or for too long from the caves. When the rains stop, the crickets are probably restricted once again to the consistently cool, humid caves. The individuals that have been found in other areas may have been relicts of the previous wet season, surviving in isolated pockets of acceptable habitat.

Affect of Predation on Habits

Many species of camel crickets use caves as diurnal resting sites (Leroy, 1967; Campbell, 1976). The apparent restriction of *Farallonophilus* crickets to caves, and the compressed activity period, may result from predation. The most important predator is likely the Farallons salamander, *Aneides lugubris farallonensis,* a subspecies of a known predator on beetles, caterpillars, isopods, centipedes and ants (Zweifel, 1949). I observed salamanders under rocks in the Rabbit Cave, as well as in cracks and hollows all over the island. Boekelheide (1976) found as many as 1950 salamanders per hectare of cliff habitat on Southeast Farallon, and Anderson (1960) estimates up to 8250 salamanders per hectare in concentrated areas. Selection pressures from predaceous, nocturnal salamanders may have condensed the crickets' activity period into the last few hours before dawn, before diurnal predators are active, but after most of the salamanders have completed their active periods. A study that confirms diet and activity period of arboreal salamanders on Southeast Farallon Island is needed.

Another likely predator is the western gull, a diurnal, broad-spectrum carnivore

(Pierotti, 1981) that would probably provide intense selection pressure for maintenance of nocturnal activity in potential prey species such as camel crickets, preventing them from expanding their active periods to include daylight hours. Southeast Farallon Island is the site of the largest western gull colony in existence (Pierotti, 1981), and all suitable land areas are occupied by the birds. Probably as a result, all large, visible insect species that prevail on the island are either nocturnal, sublithic or troglodytic. *Farallonophilus cavernicola* is all three. Diurnal orthopterans are rare on Southeast Farallon Island, although they occasionally appear. Strong easterly winds carry grasshoppers from the mainland; they have failed to establish themselves permanently despite repeated invasions and abundant grassy habitat. A likely explanation is predation by gulls.

Cassin's auklets have become the most abundant birds on the island (Ainley and Lewis, 1974) and Rentz felt that they may affect temporal activity of the camel crickets. The seabirds dig burrows in the surge caves, and all over the marine terrace, some of which are occupied by *Farallonophilus.* I noticed no interference of the crickets by the birds. I did observe the departing and returning waves of auklets, and noticed that the birds return during the peak of the crickets' activity period, when many of the insects venture outside of the caves. Auklets certainly don't eat the camel crickets: their diet consists of pelagic crustaceans and squid (Manuwal, 1974).

Conclusions

Farallonophilus cavernicola exhibits a definite circadian rhythm unique among camel crickets, with only a 2-hr activity period from 0400 to just before dawn. I hypothesize that abundant, nocturnal salamanders have delayed cricket activity until pre-dawn hours, and that activity later in the morning is restricted by predation by gulls. Insects stay hidden during the day, without moving. They are most easily disturbed after dark, indicating a higher level of alertness, but remain quiescent in their refugia until early morning. Though some crickets are solitary, most are found in groups of up to 12 individuals. *Farallonophilus* has a wider spatial distribution than previously reported, occurring in many damp, dark habitats that include at least 10 surge caves, seabird burrows, a wooden observation blind, under rocks, and elsewhere.

Acknowledgments

My study was conducted on Farallons National Wildlife Refuge, a unit of the San Francisco Bay National Wildlife Refuge Complex which is administered by the U.S. Fish and Wildlife Service. Refuge Complex Manager Rick Coleman and Wildlife Biologist Jean Takakawa approved this project as basic to an understanding of island fauna. Transportation to and from the island was provided by skippers and vessels of the Oceanic Society's Farallon Patrol. Accommodations on the island were provided by Point Reyes Bird Observatory, whose biologists serve as capable stewards and watchful guardians of Southeast Farallon. Theodore J. Cohn of San Diego State University encouraged the project, provided guidance during its ontogeny, and edited the manuscript. Christopher L. Kitting suggested further improvements. Collecting equipment was provided by the Department of Biological Sciences, California State University, Hayward. Eve Steiner raised our children, managed the household and advanced her career while I was off studying insects.

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